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INTERACTIONS BETWEEN GENOTYPE, SITE AND SILVICULTURAL TREATMENT

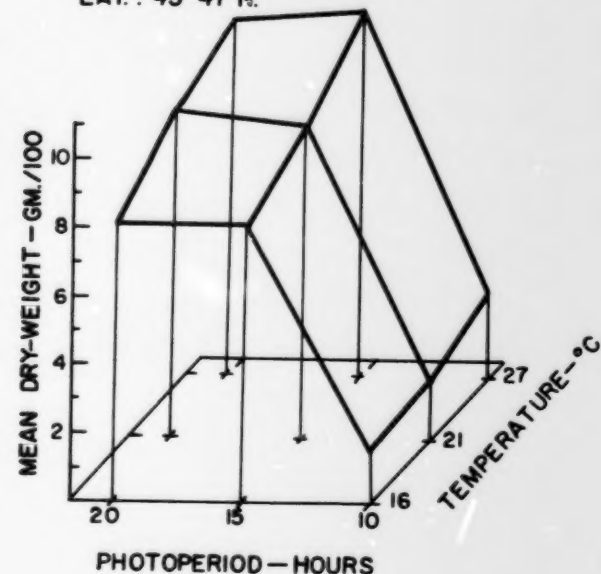
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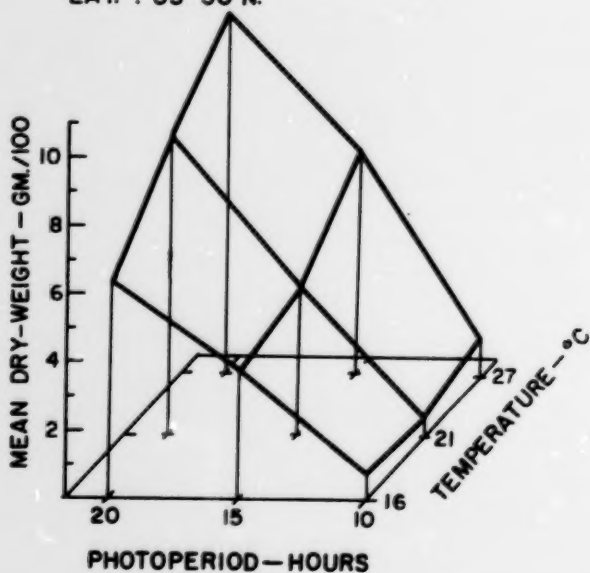
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PETAWAWA NATIONAL FORESTRY INSTITUTE

The Petawawa National Forestry Institute was formed on April 1, 1979, as the result of an amalgamation of the former Petawawa Forest Experiment Station, which had existed for more than 60 years, with the Ottawa-based Forest Management and Forest Fire Research institutes.

In common with the rest of the Canadian Forestry Service, the Petawawa National Forestry Institute has as its objective the promotion of better management and wiser use of Canada's forest resource to the economic and social benefit of all Canadians. Because it is a national institute, particular emphasis is placed on research into problems that transcend regional boundaries or that require special expertise and expensive equipment that cannot be duplicated in CFS regional establishments. Such research is often performed in close cooperation with staff of the regional centres or provincial forest services.

Research at the institute is in two main areas:

FIRE RESEARCH AND REMOTE SENSING. Every year in Canada large areas of productive forest are destroyed by fire. Research concentrates on studies of forest fire behaviour, the development of new methods of fire control, the evaluation of fire-fighting equipment and retardants, and the development of computerized fire management systems that are rapidly finding applications with fire-fighting agencies across the country. The environmental and economic impact of forest fires and the use of fire as a silvicultural tool for intensive forest management are also studied.

In remote sensing, investigations are made into the application of modern satellite and airborne remote sensing systems to forestry problems. In this respect, the ARIES digital image analysis system is proving invaluable.

INTENSIVE FOREST MANAGEMENT. As Canada moves into more intensive management of its forests to meet expected increases in demand for this important resource, the role of this program will become increasingly important. An extensive reforestation program will require a steady supply of high-quality seed of the desired species. Improved growing stock, obtained through tree breeding and forest genetics research, is highly desirable. Increased emphasis is being placed on using the entire above-ground portion of the tree (biomass), but the effect on the environment of this and other forms of intensive management has to be carefully monitored. Biotechnological methods of improving yield while maintaining site productivity are being investigated.

In support of its research programs, the institute has at its disposal a 98-km² area of forest in the northern part of the Petawawa military reserve. Records of experiments and sample plots have been maintained since the 1920s. The forest also serves as a field laboratory for students from local schools, and a visitor centre is operated during the summer months.

Cover illustration: seedling shoot dry-weight of two Pinus banksiana seed sources grown for three months in growth cabinets in combinations of three photoperiods and three temperatures, exemplifying seed source x environment interaction (from Yeatman 1966).

**INTERACTIONS BETWEEN GENOTYPE, SITE
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Information Report PI-X-14

E.K. Morgenstern

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Abstract

Interactions are considered from the viewpoint of factorial experiments in genetics and silviculture where significant interactions imply that treatments are not independent. This review is based on 38 experiments dealing with 21 species in the genera Alnus, Larix, Picea, Pinus, Populus, Pseudotsuga, and Quercus. Traits considered are: juvenile growth and phenology, color and morphology, survival and hardiness, nutrient requirements, insect and disease susceptibility, growth and yield, and spacing. Interpretation of the results depends upon an appreciation of genetic variation within the species and the particular problems of sampling and testing in each experiment. Some of the obvious factors that underlie interactions are climatic and soil differences between seed origin and test habitat and differences in genetic buffering between test populations. There are interactions that have defied interpretation but the application of special analyses and closer attention to environments should make it possible to interpret more of these difficult cases in future years.

Résumé

Les interactions de différents facteurs au cours d'expériences génétiques et sylvicoles ont été étudiées; ces interactions, lorsqu'elles sont significatives, impliquent que les traitements ne sont pas indépendants. Les résultats provenant de 38 différentes études relatives à 21 espèces des genres Alnus, Larix, Picea, Pinus, Populus, Pseudotsuga et Quercus ont servi de fondement à la présente analyse. Les traits considérés furent la croissance et les variations phénologiques des jeunes arbres, la couleur et la morphologie, la survie et la rusticité, les besoins en éléments nutritifs, la vulnérabilité aux insectes et aux maladies, la croissance et la production ainsi que l'espacement. L'interprétation des résultats dépend de l'appréciation des variations génétiques à l'intérieur d'une espèce ainsi que des difficultés d'échantillonnage et d'essai propres à chaque expérience. Parmi les facteurs évidents qui sous-tendent les interactions, il y a les différences de climat et de sol entre le lieu d'origine des graines et le lieu d'expérimentation, et les différences d'effet de tampon génétique entre chaque population d'essai. Certaines interactions n'ont pu être interprétées. Cependant, en appliquant des modes d'analyse spéciaux et en portant une attention plus grande aux différents milieux, un plus grand nombre de ces cas difficiles pourraient être interprétés au cours d'expériences futures.

INTERACTIONS BETWEEN GENOTYPE, SITE AND SILVICULTURAL TREATMENT

INTRODUCTION

Interactions between genotype, site and silvicultural treatment can take many forms and include many organisms. In a general sense, interactions mean "mutual influences", and these can involve competition between genotypes, interactions between genotypes and site factors, biotic agents, as well as silvicultural treatments. In a more specific sense, genotype x site and genotype x treatment interactions have a statistical meaning. It is this second area to which this paper will be addressed.

The subject of genotype x environment interaction is of world-wide importance because of its role wherever forests are regenerated or established. In regeneration of native species, it has a bearing on the delineation of seed zones to limit geographic seed transfer from origin to plantation environment (Campbell 1974). In afforestation trials of exotics, it must be considered to arrive at an optimum choice of seed sources (Burley and Nikles 1972, Burley and Kemp 1972). In breeding programs of any species, it complicates selection and testing and limits genetic gain. The many problems that it presents have led to much research particularly along statistical lines (see reviews by Shelbourne 1972, Shelbourne and Campbell 1976). In spite of this, it is clear that in silviculture and tree breeding, experiments with efficient experimental designs with

provision for analysis of interactions have a short history and that results are not yet available from many regions of the world.

This relative novelty of interactions is reason enough to examine their significance. Therefore, the objective of this paper is to review the impact of interactions on silvicultural and breeding programs. Emphasis will be on individual tree characters or traits that have economic importance, not on statistical problems. Some general conclusions concerning the interpretation of interactions will also be drawn.

PRINCIPLES OF INTERACTION ANALYSIS

The statistical model

Sir R.A. Fisher, who developed the analysis of variance in the early 1920's at Rothamsted Experiment Station in England, pointed out the advantages of factorial experiments: they permit the testing of several factors and their interactions at the same time (Fisher 1951).

As an illustration consider the analysis of a group of experiments with seed sources (or genotypes) repeated in a number of locations (Stern 1967). The analysis of variance is set out in Table 1.

A significant F-value for seed sources x locations means that the factors seed sources and locations are not independent of one another. The interaction could arise when there is a change in ranking of the seed sources in different locations or a change in relative superiority even when ranks are the same (Steel and Torrie 1960).

Experimental design

To make the experiment meaningful and interpretation relevant to forestry practice, it is essential that sampling and testing be carefully considered. Sampling should include seed sources from that part

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Table 1. Analysis of variance and expected mean squares of seed sources tested in two or more locations

Source of variation	Degrees of freedom	Expected mean squares
Replications in locations	$l (r-1)$	$\sigma_e^2 + \sigma_r^2/l$
Seed sources	$s - 1$	$\sigma_e^2 + r\sigma_{sl}^2 + rl\sigma_s^2$
Locations	$l - 1$	$\sigma_e^2 + r\sigma_{sl}^2 + rs\sigma_l^2$
Seed sources x locations	$(s-1)(l-1)$	$\sigma_e^2 + r\sigma_{sl}^2$
Pooled error	$l (s-1) (r-1)$	σ_e^2

r - number of replications at each location.

s - number of seed sources.

l - number of locations.

Orthogonality is assumed.

of the species' range considered suitable for the test region. Test locations within that region should be grouped or classified according to ecological parameters, and then the individual experiments distributed to them. Experiments should have appropriate numbers of replications, plot sizes and shapes, taking expected tree dimensions, space requirements and lengths of test period into account. Establishment and measurement should be done so as to avoid or eliminate confounding influences (nursery effects, transplant shocks, damage from insects and diseases, etc.). In brief, all rules for the design of seed source studies (or progeny tests) apply here (Dudley and Moll 1969, Morgenstern 1972, Wright 1976). Furthermore, suitable statistical models should be used for the analysis, and transformation of data may be necessary (Campbell and Wilson 1973, Hattemer 1965).

Interpretation of results

Interpretation of results is always dependent upon the particular conditions in each test series. Here are examples of the types of questions that the researcher must consider (Squillace 1970, Wright 1973, 1976):

Sampling and testing. Have the conditions mentioned in the preceding section been observed? If not, which limitations must be put on the interpretation?

Main effects. In all experiments, attention is first given to main effects (e.g., seed sources and locations). Even with statistically significant interactions, it is possible that some seed sources have grown well in all or most locations. These stable seed sources could then be selected. In this case interaction is of secondary importance (Matheson 1974).

Interactions. When interactions are of such magnitude that selection is seriously complicated, they may have to be analysed further. Possible solutions to the problem might be:

- Interaction variances are partitioned by calculating the contribution of individual seed sources or test environments. This could involve stability analyses using analysis of variance and regression (Wricke 1965, Eberhart and Russell 1966, Schnell 1967, Baker 1969, Utz 1972, Weiling 1973) and multi-variate techniques (Freeman

1973).

- b) Ecological conditions of the places of seed origin are compared with those of the test locations. This could include both climates and soils (Morgenstern and Teich 1969, Burdon 1971, Eiche and Andersson 1974).

In general, a knowledge of genetic variation patterns is essential for the interpretation of results.

RESULTS FOR DIFFERENT TRAITS

Examples of genotype x environment interactions from 38 experiments are summarized by trait sequence in Table 2. This is a convenient way of treating the subject of interaction in a discussion, but it is clear that in reality, for example for seed source selection, several traits must be considered at the same time. To deal with these broader questions, readers should refer to the original papers.

Juvenile growth and phenology

In a series of experiments in controlled environments with *Pinus banksiana*, Yeatman (1966) showed that there are numerous seed source x photoperiod interactions for seedling growth. There were also seed source x temperature and light intensity interactions but these were not as strong. The statistical analyses were based upon regression and a multi-variate method (canonical analysis). The same series of experiments was also subjected to analysis of variance and similar results were reported by Mergen et al. (1967).

In another study, Mergen et al. (1974) found significant seed source x temperature interactions for dry and fresh weight, height, and terminal bud frequency in *Pinus banksiana*, *Pinus sylvestris*, *Picea glauca*, and *Picea sitchensis*. Most of the interactions could be interpreted as the result of different contributions by seed sources from the various parts of the ranges of each species. Seed sources from the centre of the range were more stable than seed sources from the extremes.

In operational nurseries, genotype or seed source x environment interactions are

usually not examined. Yet these interactions are important in silviculture because the physiological differentiation of seed sources in large nurseries that produce planting stock for several ecological regions can significantly influence survival and early growth in the field (Morgenstern 1976). Working with *Pinus sylvestris*, Brown (1969) found large and significant time x seed source interactions for survival following root pruning, lifting and transplanting.

Color and morphological traits

Morphological traits are usually less influenced by environment than growth traits and therefore one could expect smaller genotype x environment interactions. This assumption is supported by the findings of King (1965 a, b) with *Pinus sylvestris*. Interactions for needle length and color were smaller than for height but still significant. The analysis of stem straightness and forking in *Pinus nigra* Arnold (Wilcox and Miller 1975) showed that interactions were small, and the authors concluded that the best seed sources could be grown throughout New Zealand.

Survival and hardiness

Survival and hardiness assume great importance where growing conditions are marginal, as in high latitudes and altitudes, or on dry sites in tropical and subtropical regions (Kemp 1973). Eiche and Andersson (1974) studied *Pinus sylvestris* in northern Sweden and found strong interactions. Cumulative mortality over a period of 20 years was large. As a consequence, seed zones or plantation zones should be narrow. The authors indicated that only seed sources from the same county could be used there. In an early report on survival and height at 6 years of *Pinus contorta* grown at 13 sites north of latitude 60 in Sweden, there were very small seed source x site interactions. However, this situation could change in subsequent years (Lindgren et al. 1976). In a study of intervarietal crosses of *Pseudotsuga menziesii* in 2 nurseries in Idaho, USA, interactions for form and

Table 2. Examples of interactions from genetic and silvicultural experiments

Species	Test materials and conditions, traits examined	Results and conclusions	Author
A. Juvenile Growth and Phenology			
<u>Pinus banksiana</u> Lamb.	50-87 seed sources from whole range in 9 controlled environments with 3 photoperiods and 3 temperatures, plus greenhouse and nursery trials; fresh and dry weight of shoots and roots, shoot length, phenology, cold hardiness and other characters; 2-12 months after sowing.	Significant seed source x photoperiod, temperature and light intensity interactions.	Yeatman 1966, Mergen et al. 1967
<u>Pinus banksiana</u> <u>Pinus sylvestris</u> L. <u>Picea glauca</u> (Moench) Voss <u>Picea sitchensis</u> (Bong.) Carr.	47 seed sources (11-12 from each species) in growth cabinets; 6 temperatures; dry and fresh weight, height, and frequency of terminal buds; 3 months after sowing.	Most temperature x seed source interactions were significant. Seed sources from central parts of the ranges usually contributed least to the interaction.	Mergen et al. 1974
<u>Pinus sylvestris</u>	5 seed sources from S-N gradient in Europe, selected in nursery 1 month after germination, root pruned and analyzed at monthly intervals; survival and root characters in 1st year.	Significant time x seed source interactions for survival.	Brown 1969
<u>Pinus sylvestris</u>	50-100 seed sources from whole range on 8 field sites in Illinois and Michigan; needle length, color, height at 4-5 years.	Significant site x seed source interactions for height; interactions for needle length and color also significant but much smaller.	King 1965a, 1965b
B. Color and Morphological Traits			

Table 2. (cont'd)

Species	Test materials and conditions, traits examined	Results and conclusions	Author
<u>Pinus nigra</u> Arnold	43 seed sources on 6 sites in New Zealand; volume, diameter, height, straightness and forking at 19 and 20 years.	Source x site interactions considered spurious because of single plots on some sites; little change in ranking.	Wilcox and Miller 1975
C. Survival and Hardiness			
<u>Pinus sylvestris</u>	100 seed sources from Sweden, Germany and Holland tested on 6 sites in northern Sweden; survival and height 1-19 years after planting.	Interaction not analyzed in standard manner, but appeared to be strong.	Eiche and Andersson 1974
<u>Pinus contorta</u> Dougl.	83 seed sources from whole range tested on 13 sites north of latitude 60° in Sweden; mortality and height at age 6 years.	Interaction not examined in detail at this early stage but did not appear to be strong.	Lindgren et al. 1976
<u>Pseudotsuga menziesii</u> (Mirb.) Franco	103 families of full-sibs from intervarietal crosses and parental lines in 2 nurseries; growth, phenology, hardiness at 4 years.	Nursery x family interactions were significant only for tree form, frost damage.	Rehfeldt 1977
D. Nutrient Requirements			
<u>Picea glauca</u>	12 seed sources from Ontario and Michigan; 1 field test on granitic and 1 on calcareous site within 50 km in Ontario; height, 15 years.	Significant source x site interaction. Advocate to use granitic origin sources on granitic and calcareous on calcareous sites.	Teich and Holst 1974

Table 2. (cont'd)

Species	Test materials and conditions, traits examined	Results and conclusions	Author
<u>Pinus radiata</u> D. Don.	18 clones planted out as cuttings on 4 sites in New Zealand; height, diameter and stem traits, 12 years after establishment.	Found marked clone x site interactions for branching frequency and stem straightness which were related to phosphorus deficiency. Tolerance to P deficiency seemed to be clone specific.	Burdon 1971
E. Insect and Disease Susceptibility			
<u>Pinus sylvestris</u>	20 seed sources from western part of range on 10 sites in Germany; infection by needle cast, <u>Lophodermium pinastri</u> (Schrad.) Chev.; age 2-4 years.	Significant seed source interactions with sites and years.	Hattermer 1965
<u>Pinus elliotii</u> <u>var. elliotii</u> Engelm.	54 seed sources from whole range; 4 sites in Florida, Georgia, Mississippi; survival, height, diameter, gum yield, and infection by fusiform rust, <u>Cronartium fusiforme</u> Hedge. Hunt ex Cumm.	Significant seed source x site interaction for height and fusiform rust, but rust interaction showed no clear pattern.	Gansel et al. 1971
<u>Pinus banksiana</u>	26 seed sources from Minnesota, Wisconsin, Michigan tested on 11 sites in these States; infestation by the white pine weevil (<u>Pissodes strobi</u> Peck), shoot borer (<u>Eucosma gloriola</u> Heinrich) and gall rust (<u>Cronartium quercum</u> (Berk) Miyabe ex Shirai), ages 7 or 12 years.	Significant seed source x site interactions for all 3 pests. But overall impact of pests small.	King 1971

Table 2. (cont'd)

Species	Test materials and conditions, traits examined	Results and conclusions	Author
F. Growth and Yield:			
<u>Populus hybrids</u>	16 hybrid clones on 13 sites in Germany; height at 4 years.	i) Clones Clone x site interaction not tested for significance but variance component about equal in magnitude to clone component.	Hattermer et al. 1964
<u>Populus deltoides</u> Bartr.	50 clones at 3 sites in Illinois; height and diameter at 1-5 years.	Clone x site interactions significant. Mississippi clones grew better than Illinois clones.	Randall 1973
<u>Populus deltoides</u>	25 clones in 6 plantations in Mississippi (2 sites x 3 years); height, diameter and branch number, 1-3 years.	Small clone x year and large clone x site interactions.	Mohn and Randall 1973
<u>Picea abies</u> Karst.	51 clones from several elevations in Austria tested at 4 sites, 850 m, 1250 m, 1600 m, and 1900 m; cuttings at age 4 years; height, and dates of growth initiation and cessation.	Clone x site interactions appeared to be small (not analyzed in standard manner).	Lechner et al. 1977
<u>Pinus elliottii</u> var. <u>elliottii</u>	6-10 progenies tested on 3 sites in Georgia; height, fusiform rust infection, crown width/height ratio 5 years after planting.	ii) Progenies Interaction significant only for height and crown/height ratio.	Kraus 1970

Table 2. (cont'd)

Species	Test materials and conditions, traits examined	Results and conclusions	Author
<u>Pinus patula</u> <u>Schiede & Deppe</u>	Numerous progenies from controlled crosses on 4 sites in eastern Rhodesia; about 30 traits related to growth, stem and branch morphology; measurements 1 1/2 years after planting.	Few of the interactions were significant. Interactions are not important in the selection program.	Barnes 1973
<u>Pinus radiata</u>	28 progenies on 3 sites in Victoria, Australia; height at 7 years.	Progeny x site interaction significant and having influence on selection strategy.	Pederick 1972
<u>Picea mariana</u> (Mill.) B.S.P.	28 progenies from local area in Ontario; 1 dry and 1 moist nursery site; height, 4 years.	Significant progeny x site interaction. Selection on individual sites not effective.	Morgenstern 1973, 1974
<u>Pinus banksiana</u>	100 progenies from several stands in Ottawa Valley, Ontario; 3 sites within 50 km; height at 6 years.	Neither site x progeny nor site x stand interaction significant. Selection could be based on testing at a single site.	Yeatman 1974
<u>Pinus virginiana</u> Mill.	138 progenies from 13 stands in Kentucky and Tennessee on 5 sites in Tennessee and Alabama; volume production 5 years after planting.	Interactions of progenies and stands with sites were significant but accounted for less than 1% of total variance.	Rink and Thor 1976
<u>Picea glauca</u>	42 progenies from local area on 3 sites within 16 km in Ontario; height, 10 years.	Progeny x site interactions not significant. Experimental design not satisfactory.	Dhir 1975

Table 2. (cont'd)

Species	Test materials and conditions, traits examined	Results and conclusions	Author
<u>Alnus glutinosa</u> L. Gaertn.	16 progenies from controlled crosses on 4 sites in Saxony, Germany; height at 4 years.	Progeny x site interaction significant.	Thomasius 1967
<u>Alnus glutinosa</u>	33 progenies from controlled crosses, open pollination, and selfing on 4 sites in Hesse, Germany; height at 7 years.	Progeny x site interaction significant.	Weissgerber 1974
iii) Intervarietal Crosses and Introgressed Populations			
<u>Picea rubens</u> Sarg. and natural hybrids with <u>Picea mariana</u>	12 seed sources from whole range; 3 field tests within 160 km in Ontario; survival and height, 12 years.	Limited changes in rank and interaction variance component small.	Morgenstern 1969
<u>Picea rubens</u> and natural hybrids with <u>Picea mariana</u>	15 seed sources from whole range; 3 field tests within 160 km in Quebec; height, 13 years.	Seed source x environment interaction not significant.	Roche 1969
<u>Pinus monticola</u> Dougl.	31 progenies including intervarietal crosses on 2 sites in Idaho; height at 9 and 14 years.	Progeny x site interactions significant only at 9 years, and interpreted as negligible.	Rehfeldt and Steinhoff 1970
iv) Seed Sources			
<u>Larix leptolepis</u> Gordon	25 seed sources on 13 sites in Germany; height, diameter and mortality; ages 3-9 years.	Large seed source x site interactions which were considered the result of the large difference between native and culture environments.	Hattermer 1969

Table 2. (cont'd)

Species	Test materials and conditions, traits examined	Results and conclusions	Author
<u>Picea abies</u>	16 seed sources from western part of range; 3 field tests in eastern France, latitude 43-48°N, elevation 1000-1600 m; phenology and height, 2-12 years.	Changes in rank imply source x site interaction for height.	Lacaze 1970
<u>Picea abies</u>	36 seed sources of the IUFRO 1938 study on 25 sites in Europe and North America; height 12-30 years.	Interactions not estimated quantitatively but noticeable particularly as a result of source differentiation on northern and southern test sites.	Giertych 1976
<u>Picea glauca</u>	29 seed sources from whole range; 14 sites from North Dakota, U.S.A., to New Brunswick Canada; height, 9 years.	Significant source x site interaction, but best sources changed little in rank.	Nienstaedt 1969
<u>Pinus banksiana</u>	16 seed sources from Minnesota, Wisconsin, Michigan on 12 sites in these States and Ontario; height 12 years.	Contributions of individual seed sources to interaction depended upon distance moved from origin to test site.	Morgenstern and Teich 1969 (based partly on data given by King 1966).
<u>Pinus taeda</u> L. and <u>Pinus echinata</u> Mill.	Several series of experiments established throughout southeastern United States; height 10- or 15 years.	Seed source x site interaction arose from different performance of seed sources on northern and southern test sites.	Wells 1969

Table 2. (cont'd)

Species	Test materials and conditions, traits examined	Results and conclusions	Author
<u>Quercus rubra</u> L.	4 seed sources from different elevations in North Carolina sown at 4 test sites in same area; height and phenology in 2nd year.	Seed source x site interaction very small and probably not significant (not analysed in standard manner).	McGee 1974
G. Reaction to Silvicultural Treatment: Spacing			
<u>Pinus sylvestris</u>	55 seed sources from east-central Europe; 1 site with a replicated test in NW Germany, with 2 spacings, 0.3 x 0.3 m and 1.0 x 1.0 m; survival height, diameter, stem form, and branchiness at 16 years.	Seed source x spacing interaction significant only for survival.	Mathieu 1967
<u>Pseudotsuga menziesii</u>	30 progenies from controlled crosses in nursery test in Oregon, spacing 2.5, 7.5, 12.5 and 17.5 cm with 4 replications; heights and root-collar diameters at 3 years. Results were compared to those from 43-year-old trees.	After transformation of data, progeny x spacing interactions were not significant. There were no changes in rank but survival differed.	Campbell and Wilson 1973

frost damage were significant even in 4-year-old trees (Rehfeldt 1977).

The problem of seed zoning from the viewpoint of genotype x environment interactions has been discussed in detail by Campbell (1974) and Shelbourne and Campbell (1976).

Nutrient requirements

The potential significance of nutrients for seed source differentiation and the possibility of soil ecotypes had been realized for some time but very little experimental evidence was available until recently (Stern and Roche 1974). In a study of Picea glauca, seed source x planting site interactions were highly significant. The interpretation given was that both seed source localities and test sites differed with respect to calcium content of the soil. Seed sources from calcareous soils performed better on calcareous test sites and sources from acid soils better on acid sites (Teich and Holst 1974). Deficiencies in phosphorus (P) have also led to marked interactions in Pinus radiata. Some clones of this species were unable to cope with P deficiencies and formed abnormal stems and branches (Burdon 1971). Zobel and Roberds (1970) have indicated that nutrient interactions at the level of progenies are more numerous than initially expected. Squillace (1970) has cited many interactions related to fertilizer effects.

Susceptibility to insects and diseases

Hattermer (1965) found significant seed source x site and seed source x year interactions in Pinus sylvestris infected by the needle cast fungus (Lophodermium pinastri). Gansel et al. (1971) discovered that in Pinus elliotii scored for infection by fusiform rust (Cronartium fusiforme), there were strong seed source x site interactions. In both cases, the interpretation of the results was difficult, and probably complicated by the presence of several physiological races of the fungus. However, Hattermer (1965) was able to subdivide the seed sources into 4 geographic groups based upon their mean susceptibility ratings and contribution to interaction. No geographic trends were

evident in Pinus elliotii but variation in pathogenicity of several fungus races has subsequently been confirmed (Snow et al 1975). There were also significant seed source x site interactions for incidence of eastern gall rust (Cronartium quercum) on Pinus banksiana (King 1971).

King has also investigated susceptibility to two insects, white pine weevil (Pissodes strobi) and the eastern pine shoot borer (Eucosma gloriola). Significant seed source x site interactions were found for both insects but were not examined in detail (King 1971).

Growth and yield

One of the prerequisites of good growth and yield is general adaptability of the tested populations. Adaptability usually increases with genetic diversity (Allard 1964, Fejer 1967). This is the reason why interactions for growth and yield can profitably be discussed separately for different levels of genetic diversity, i.e., for clones, progenies, intervarietal crosses, and seed sources.

Clones. All members of a clone are genetically uniform and variation among clones is therefore the most basic kind. With one exception the clonal tests listed in Table 2 showed strong interactions. For Pinus radiata, there were significant clone x site interactions for height and diameter and these seemed to be closely related to a clone-specific reaction to phosphorus as discussed earlier (Burdon 1971). Sizable clone x site interactions were also found for Populus hybrids (Hattermer et al 1964) and for Populus deltoides by Mohn and Randall (1973) and Randall (1973). The clonal test of Picea abies discussed by Lechner et al (1977) was not subjected to analysis of variance but illustrations indicated that interactions, if present, may have been small. Origin from a narrow altitudinal range could be the explanation.

Progenies (either from open or controlled pollination) constitute the next higher level of variation, being less uniform than clones, and possibly more strongly

buffered to cope with environmental variation. However, many of the tests in this category were marked by significant interactions with site, namely those for Alnus glutinosa (Thomasius 1967, Weissgerber 1974), Pinus elliotii (Kraus 1970), Pinus radiata (Pederick 1972), and Picea mariana (Morgenstern 1973, 1974). In contrast, tests of Pinus banksiana (Yeatman 1974), Picea glauca (Dhir 1975), and Pinus virginiana (Rink and Thor 1976) revealed non-significant interactions. It appears that the tests with Pinus banksiana and Pinus virginiana were conducted in a realistic manner with respect to sampling and distribution of tests to sites. As a result, progeny selection would be relatively simple and be based largely on main effects, i.e., the best progenies in the whole test series, provided that present trends continue. The progeny tests of Pinus patula yielded similar results with interactions for only a few traits and few changes in rank, but the author concluded that test site selection could be improved in the future (Barnes 1973).

Intervarietal crosses and introgressed populations. Again this is a group that is buffered more than the previous one. The results in Table 2 support this theory, for neither the Picea rubens provenances containing introgressed populations (Morgenstern 1969, Roche 1969) nor the Pinus monticola intervarietal crosses (Rehfeldt and Steinhoff 1970) showed substantial interactions.

Seed sources usually contain much variability within them due to their origin from many trees, and could therefore be relatively stable from site to site, showing little interaction. Nevertheless, when seed source tests are distributed widely, interactions are common. Morgenstern and Teich (1969) showed that in Pinus banksiana the regression of total height on latitude of seed origin had opposite trends at the northernmost and southernmost test sites, with the regression coefficient being positive in the north and negative in the south. Stability analyses indicated that the seed sources from the extreme north and

south contributed most to the interaction variance. A similar situation was reported for Picea abies by Giertych (1976). The close adaptation of northern tree species to native photoperiods and temperature regimes is part of the explanation. Even in southern species (Pinus taeda and Pinus echinata), where climatic gradients are not as steep, a similar reaction was found (Wells 1969). When testing on sites along elevational gradients, this reversal of the position of seed sources was again evident in Picea abies (Lacaze 1970) but not in Quercus rubra (McGee 1974). In Larix leptolepis experiments, there were large interactions but interpretation was difficult. It was proposed that the large ecological difference between native areas and test sites called forth a great deal of new variability (Hattermer 1969). However, even if significant interactions have taken place, high yielding seed sources with sufficient stability can be found and selected as shown for Picea glauca by Nienstaedt (1969).

Reaction to silvicultural treatment:

Spacing

Mathieu (1967) considered effects of two spacings (0.3 x 0.3 m and 1.0 x 1.0 m) on Pinus sylvestris seed sources, using survival, height, diameter, stem form and branchiness as criteria. A single test site was used but the treatments were replicated. Among the seed source x spacing interactions, only those for survival were statistically significant. Campbell and Wilson (1973) found that in a nursery experiment with Pseudotsuga menziesii, progeny x spacing interactions for height and diameter were not significant after transformation of the data to achieve normality.

It appears that forest genetic experiments using spacing as a factor are rare although effects of spacing on growth have been well investigated from a silvicultural point of view (Burgan 1971, Low and van Tol 1974). Spacing and competition can have large consequences and need to be investigated further (Adams et al 1973, Stern and Roche 1974).

CONCLUSIONS

Interactions between trees and environments are common for many traits, but overall comparisons of the impact of interaction on different traits based on strict quantitative criteria such as significance of F-values or variance components can be made only to a very limited degree. Significance merely implies that interactions have been precisely estimated and not necessarily that they are important. While the relative sizes of variance components of interaction and genetic effects are more instructive (Squillace 1970), they also have their limitations. Conditions of sampling and testing are often not comparable.

From the preceding results, it is possible to list a number of factors that underlie many of the interactions:

- a) Climatic differences between old (parental) and new (progeny = test) environment. These differences consist of a change in photo- and thermo-period (length of growing season) and are expressed by variation in survival, growth rhythm, and insect and disease susceptibility at different ends of the spectrum of environments included in a test series (Hattemer 1965, Morgenstern and Teich 1969, Eiche and Andersson 1974, Mergen et al 1974). The study by Hattemer (1969) also belongs into this category but is a special case.
- b) Soil differences between old and new environment. Here genotypes or seed sources are site specific so that they cannot tolerate certain nutrient conditions (deficiencies) or are less vigorous than in their original habitat (Burdon 1971, Teich and Holst 1974).
- c) Differences in genetic buffering of the tested populations. Some genotypes or seed sources appear to be broadly adapted to a range of sites (stable genotypes) while others are adapted more narrowly. In general, buffering increases from genotypes (or clones) to

progenies to intervarietal crosses and seed sources (Nienstaedt 1969, Roche 1969, Pederick 1972, Randall 1973, Yeatman 1974).

In addition to these factors, there must be others that have not been recognized. For many species, experiments have only been recently established and results are not yet available. The advantages of factorial experiments to analyse the genotype x environment interaction have been pointed out (Burley and Kemp 1973) and these should be recognized everywhere. In general, it seems obvious that geneticists have not paid enough attention to environments and that many interactions will likely be interpretable once this is done.

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